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Trissopathes (Anthozoa: Antipatharia) in the north-east Atlantic, with a description of *T. grasshoffi* . sp. nov.

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Abstract

A new species of antipatharian (black coral) in the genus *Trissopathes* is described. It is common in the bathyal zone of the north-east Atlantic, including the Bay of Biscay, Celtic Slope and adjacent banks and seamounts. The species is often observed in underwater photographs from untrawled parts of carbonate mounds in the area. *Trissopathes grasshoffi* sp. nov. can be easily distinguished from its three congeners by having relatively sparse branching, a higher density of primary pinnules, and 3–6 secondary anterolateral pinnules as well as by the shape and size of its spines. The present state of knowledge of *Trissopathes* is reviewed.

Key words: Cnidaria, Cladopathidae, deep-sea coral, marine taxonomy

Running title: *Trissopathes* from the north-east Atlantic

Introduction

For most parts of our planet the deep sea remains unexplored, yet the benthos of the north-east Atlantic has been sampled extensively, starting with sampling of deep Norwegian fjords by Michael Sars in the 1830's followed by a series of surveys of the continental slope starting with HMS *Lightening* in 1868 (Rozwadowski 2005). Black corals (Antipatharia) are one of the most spectacular types of organisms found in the deep sea, as they are widely distributed (Yesson *et al.* 2012), can be metres in length and thousands of years old (Roark et al. 2009). They get their name from beliefs dating back to the 14th Century that they are effective charms against harm, '*pathos'* being Greek for 'suffering'. Their common English names are 'black corals' or 'thorny corals' because their skeleton is a beautiful lustrous jet black or dark-brown in colour and covered in minute spines. Currently 37 species of black corals have been reported from the northeast Atlantic north of Oceanographer Fracture Zone (Molodtsova 2006a, 2011, 2014, 2016, Braga-Henriques *et al*. 2013, de Matos *et al*. 2014), although this is probably an under-estimate.

In the last few decades Remotely Operated Vehicle surveys of the north-east Atlantic have intensified. These surveys show that antipatharians can be common in areas that have not suffered trawling damage, particularly on carbonate mounds (Davies *et al*. 2007, Roberts *et al*. 2008, Wienberg *et al*. 2008, Narayanaswamy *et al*. 2013, Davies *et al.* 2014, Van Den Beld *et al*. 2017, De Clippele *et al*. 2019). In these and other surveys an undescribed species of the genus *Trissopathes* Opresko, 2003 was repeatedly observed, and sometimes collected from the bathyal zone of the Bay of Biscay, Celtic Slope and adjacent banks and seamounts (Altuna 2014, Instituto Español de Oceanografía, 2014a, b, Sánchez *et al*. 2014, Van Den Beld *et al*. 2017, De Clippele *et al*. 2019). Study (TM) of previously published (Grasshoff 1982a, b) material deposited in MNHN revealed that the same species was also reported as *Antipathes* sp. from the Bay of Biscay. The main propose of the present work is to formally name and describe this new species and to discuss the composition and the present state of knowledge of the genus *Trissopathes.*

Abbreviations and Acronyms Used

BobEco – the Bay of Biscay Ecology cruise (RV *Pourquoi Pas?* September-October 2011)

CP – beam-trawl

CM – Marinovich trawl

ECOMARG – Estudio de los ecosistemas del margen continental e impacto de sus pesquerías (Study of Continental Margin Ecosystems and the Impact of Their Fisheries) FV – fishery vessel

IEO – Instituto Español de Oceanografía

Ifremer – Institut français de recherche pour l'exploitation de la mer

INDEMARES – Inventario y designación de la Red Natura 2000 en áreas marinas del Estado español

IORAS – Shirshov Institute of Oceanology of the Russian Academy of Sciences, Moscow, Russia

MNCN – Museo Nacional de Ciencias Naturales, Madrid, Spain

MNHN – Muséum national d'Histoire naturelle, Paris, France

NHMUK– Natural History Museum, London, UK

PL – Dive

RV – research vessel

RMNH –Naturalis Biodiversity Center, Leiden, the Netherlands

SAMS – the Scottish Association for Marine Science, Oban, UK

SEM – Scanning Electron Microscopy

USNMHN – National Museum of Natural History, Smithsonian Institution, Washington, DC, USA

ZMA – Instituut voor Taxonomiche Zoölogie, Amsterdam, the Netherlands (currently in Naturalis Biodiversity Center)

Material and methods

Specimens were initially preserved dry or were fixed in 4 % seawater buffered formaldehyde and then transferred to 70 % alcohol. Our measurements were carried out on preserved material. The inner angle between the two rows of anterolateral or posterolateral primary pinnules was chosen as formed by polypar sides of corresponding pinnules. The spines were measured using light microscopy and SEM of the skeleton. The distance between spines was chosen as a distance measured between centers of the bases of adjacent spines in the same longitudinal row; the height of the spine was chosen as a distance between the apex and the center of the base of the same spine. Polyp diameter was chosen as a distance measured between the distal edge of the distal lateral tentacles to the proximal edge of the proximal lateral tentacles.

Holotype and paratypes were deposited in MNHN and MNCN. Schizoparatypes were deposited inNHMUK, reference collections of Ifremer (Brest) and IORAS .

Type specimens of *Trissopathes pseudotristicha* Opresko, 2003 (holotype USNM 98848; schizoholotype, RMNH Coel. 32045), *T. tetracrada* Opresko, 2003 (schizoholotypes USNM 99399, RMNH Coel. 32043) and *Parantipathes* (?) *tristicha* van Pesh, 1914 (ZMA Coel. 3005) were studied for comparison.

Results

Systematic description

Cladopathidae Kinoshita, 1910

Hexamerota Schultze, 1896: 12

Cladopathinae Kinoshita, 1910: 231

Cladopathidae Opresko, 2003: 496; 2005:156; Opresko & de Laia Loiola 2008: 50

Diagnosis: Polyps with six primary mesenteries but no secondary mesenteries. Actinopharynx may be present or absent. Polyps elongated transversely in direction of axis; transverse diameter 1.5–6 mm, as measured from distal edge of distal lateral tentacles to proximal edge of proximal lateral tentacles. Corallum monopodial or branched, and pinnulate. Pinnules simple or with one or more orders of subpinnules. Spines conical to acicular, smooth-surfaced, subequal around the circumference of the axis, or taller on polypar side, often more strongly developed on anterior pinnules or subpinnules (Opresko, 2003).

Remarks: Opresko (2003) proposed three subfamilies: Cladopathinae, Sibopathinae and Hexapathinae based on morphological characters. Recently, the validity of the genus *Sibopathes* van Pesch, 1914 was questioned (Brugler *et al*. 2013) based on molecular data on several non-type specimens of the species *S. macrospina* Opresko, 1993 (non-type species of the genus). Further studies to support validity and composition of subfamilies Hexapathinae, Cladopathinae and Sibopathinae are needed using both morphological and molecular characters.

Trissopathes Opresko, 2003

Parantipathes [partum] van Pesch, 1914: 23, 96

Antipathes [partum] Grasshoff, 1982a: 742; 1985: 303

Trissopathes Opresko, 2003: 502; Brugler *et al*. 2013: 316

not *Parantipathes* Brook, 1889: 141–142

Diagnosis. Primary pinnules arranged in four regular rows; subequal in size or with lateral/posterolateral primary pinnules longer than anterior ones. Lateral/posterolateral primary pinnules arranged alternately and usually without subpinnules; anterior/anterolateral primaries simple or with up to six, rarely more subpinnules. Subpinnules commonly arranged in subopposite pairs or alternating.

Type species. *Trissopathes pseudotristicha* Opresko, 2003

Remarks. Younger unbranched specimens of *Trissopathes* and *Heteropathes* Opresko, 2011 could be hard to distinguish morphologically which may explain why some specimens identified as species of these two genera showed no genetic differences when analyzed using several mitochondrial markers (Brugler *et al*. 2013) Study of the holotype of *T. tristicha* (van Pesch, 1914) revealed that the colony 9 cm high has a morphology very close to that described for *Heteropathes*: subopposite lowermost pair of posterolateral pinnules and striatum extended from the lower part of the stem to 3rd posterolateral pinnules. Also all hitherto known species of both genera have reproductive polyps restricted to the anterolateral row of pinnules (Opresko 2003, 2005; Molotsova 2006b). However, all of hitherto known species of *Trissopathes* have anterior/anterolateral pinnules subpinnulated predominantly in one plane with only secondary subpinnules present (Opresko 2003, Table 1) and often with assymetrically developed basal pair of secondary pinnules. In contrary, species of genus *Heteropathes* have more intensively subpinnulated anterior pinnules with tertiaries arranged on upper and lower sides and more or less symmetrically developed lowermost pair of secondary pinnules (Opresko 2003, 2005; Molodtsova 2016).

Species assigned to *Trissopathes*. *Trissopathes pseudotristicha* Opresko, 2003; *T. tetracrada* Opresko, 2003; *Parantipathes tristicha* van Pesh, 1914; *T. grasshoffi* sp. nov.

Distribution. Species of this genus have been found in the central and eastern North Pacific (*T. pseudotristicha*), the Indo-West Pacific (*T. tristicha*), the Great Australian Bight and the Tasmanian seamounts (*T. tetracrada*), and the eastern North Atlantic (*T. tetracrada, T. grasshoffi* sp. nov.) (van Pesch 1914, Grasshoff 1982a, b; Opresko 2003; Altuna 2010; Narayanaswamy *et al*. 2013; Sánchez *et al*. 2014; Van Den Beld *et al*. 2017; De Clippele *et al*. 2019). The reported depth range is 280–2220 m.

Trissopathes grasshoffi **sp. nov. (Figures 1—4, Tables 1—2)**

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Antipathes spec., Grasshoff 1982a: 742, 1982b: 963, fig. 50–51; 1985: 303

Parantipathes sp., Narayanaswamy *et al*. 2013: fig. 2d

Trissopathes n. sp., Altuna 2010: 18, 2015: 35

Trissopathes sp., Altuna 2014: 168; Instituto Español de Oceanografía 2014a: 113, 2014b: 111, 112, fig. 75; Sánchez *et al*. 2014: fig. 15C; Van Den Beld *et al*. 2017: 14; De Clippele *et al*. 2019: 6–8

Material studied:

Holotype. MNHN-IK-2015-2212, RV *Pourquoi Pas?*, BobEco ROV *Victor 6000* PL 469-47-7, Guilvinec Canyon, 46°56.197'N–005°21.252'W, 928 m, 18.09.2011.

Paratypes: MNCN 2.04/2026, RV *Cornide Saavedra*, ECOMARG 2009, Galicia Bank, Stn. G05, 42º28.398'N–11º28.47'W, 859 m, 23.07.2009; MNHN-IK-IK-2015-2214, RV *Pourquoi Pas?*, BobEco ROV *Victor 6000* PL 468-46-6, Croizic Canyon, 46°22.864'N–004°0.740'W, 849 m, 17.09.2011; MNHN-IK--2015-2215, RV *Pourquoi Pas?*, BobEco ROV *Victor 6000* PL 469-47-7, Guilvinec Canyon, , 46°56.024'N–005°21.621'W, 834 m, 19.09.2011.

Ifremer Brest, reference collection no number (schizoparatypeNHMUK 2019. 29; schizoparatype IORAS CNI00013), RV *Polarstern* ARK-XIX-3a, Stn. PS64/293-1, ROV *Victor 6000*, Porcupine Bank, Giant Mounds, 53°11.55'N–14°47.13'W, 760 m, 14.06.2003; Coll. J. Hall-Spencer

Additional material (see Table 1)

Diagnosis. Corallum bushy or almost planar, sparsely and irregularly branched to the third order or more; stem and branches pinnulate and subpinnulate (Fig. 1A, B). Primary pinnules arranged in four rows, two anterolateral and two posterolateral, and also arranged alternately in bilateral groups containing one anterolateral and one posterolateral pinnule (Fig. 1B). There are 14–16 primary pinnules per centimeter, counting pinnules in all rows. Posterolateral primary pinnules mostly 10–18 mm long (up to 20–26 mm) and longer than anterolateral primary pinnules (5–10 mm long). Posterolateral primary pinnules directed distally; anterolateral primary pinnules directed nearly at right angles to direction of branch with very narrow inner angle (20–30°) (Fig. n2A, 2C). Secondary pinnules on anterolateral primary pinnules, occurring in subopposite pairs or almost subalternately (Fig. 2). Generally there are one to three (mostly two or three) pairs of secondary pinnules on each anterolateral primary pinnule (Fig. 1D–E, 2A–G). Secondary pinnules 5–15 mm long; proximal pair is the longest and often asymmetrically developed. Secondary pinnules lying in the same plane as anterolateral primary pinnules on which they occur, with exception of the most distal secondary pinnule that can be unpaired and offset from the plane. . Tertiary pinnules absent. Spines on pinnules (Fig. 3A–C, 4A–C) simple, smooth, conical, compressed, with straight distal side, inclined distally; 0.04–0.05 mm tall (from center of base to apex) near the base of pinnules and subpinnules and up to 0.22–0.25 mm near distal ends of primary and secondary pinnules (Fig. 1E, 3A–C, 4A–C); arranged in rows, with 3–5 rows visible in side view); mostly 0.3–0.7 mm apart in each row, with two to four spines per millimeter in each row. Polyps (Fig. 1B–D) 2.0–3.5 mm in transverse diameter; arranged

uniserially on upper or lateral sides of pinnules and subpinnules, with two to three polyps per centimeter. Polyps with sexual products are restricted to anterolateral pinnules. In underwater photographs and in freshly preserved material soft tissue is dark-red.

Description of the holotype (Figures 1A–E, 3A–C).

The holotype is a complete colony 24 cm high and 18 cm wide with holdfast 0.9 cm x 1.3 cm covered by small spines and attached to a dead fragment of the scleractinian coral *Lophelia pertusa* (Linnaeus, 1758). (Fig. 1A). The main stem is 16 cm long (3.5 x 4 mm in diameter near the base, slightly compressed laterally) and gives rise to 10 side branches 3 to 24 cm long (basal diameter 0.5 to 2 mm); some of them have 1–2 orders of secondary branches. The corallum is branched mostly up to third order. The length of ultimate branches is 3–6 cm, but some reach up to 14–20 cm.

Stem and branches pinnulate and subpinnulate (Fig. 1B) with lower 0.8–2.0 cm of stem and branches free of pinnules. Primary pinnules arranged in four rows, two anterolateral and two posterolateral, and also arranged alternately in bilateral groups containing one anterolateral and one posterolateral pinnule. Anterolateral pinnules arranged at the same level or just below corresponding posterolateral pinnule of the same group. Posterolateral primary pinnules are 2.5–3 mm apart in each row with 4–4.5 (up to 5) pinnules per 1 centimeter on each side. The interior angle between posterolaterals is 250–300°. The anterolateral primary pinnules are only slightly offset with interior angle 20–30° and very closely set. There are 13–16 (up to 17) primary pinnules per centimeter, counting pinnules in all rows.

Posterolateral primary pinnules (Fig. 1B) mostly 10–17 mm long (up to 20–22 mm) and 0.25–0.45 mm in diameter near the base. They are more or less straight and directed distally with a distal angle to stem or corresponding branch of 50–60°. Posterolateral pinnules are usually simple, secondary pinnules found on only posterolateral pinnules transforming into secondary branchlets.

Anterolateral primary pinnules (Fig. 1B, D, E) mostly 6–9 mm long and 0.36–0.45 mm in diameter near the base, almost perpendicular to the stem and branches or slightly inclined distally with distal angle 80–90° (Fig. 1B). Up to five secondary pinnules per anterolateral primary pinnules. Secondary pinnules 0.5–1.5 cm long, often asymmetrically developed with longer pinnules on the side of corresponding to posterolateral pinnule of the same group. Usually two basal subpinnules are subopposite and others can be subopposite or almost alternate. However, secondary pinnules are lying in the same plane as the anterior primary pinnules on which they occur. Tertiary pinnules absent.

Spines on pinnules (Fig. 3A–C) are simple, smooth, conical, compressed, acute; 0.03–0.24 mm tall (from center of base to apex), subequal in size around circumference of axis or slightly

taller at polypar side, taller (0.17–0.24 mm vs. 0.03–0.1 mm) and more inclined distally (40–60°vs. 60–80°) near the distal ends of the primary and secondary pinnules (Fig. 3 A–C). The spines on the pinnules are arranged in rows along length of the axis, with three to four, rarely five rows visible in lateral view. The distance between adjacent spines in each row mostly 0.3–0.7 mm, resulting in two to four spines per millimeter in each row.

Polyps on the holotype are exceptionally well preserved (Fig. 1C, D). Polyps on the posterolateral pinnules are elongated along the traverse axis; the distance from the distal edge of distal lateral tentacles to proximal edge of the proximal lateral tentacles ranges from 1.8 to 2.2 mm. They are arranged uniserially on upper or lateral side of the pinnule 1–2 mm apart, with up to three polyps per centimeter. Polyps on the anterolateral pinnules (Fig. 1D) are 2.0–2.6 mm in transverse diameter, they are mostly arranged one per pinnule or subpinnule, asymmetrically developed with swelled proximal part adjacent to the point of attachment of the subpinnule. There are no polyps on the primary anterolateral pinnules between the subpinnules.

Paratypes. MNHN-IK-2015-2214 and MNHN-IK-2015-2215 are smaller colonies that closely resemble the holotype in colony structure, arrangement of pinnules and form of spines. Some of posterolateral pinnules of MNHN-IK-2015-2215 reach 22–24 mm. Paratype from the reference collection of Ifremer Brest is 41 cm high and 22 cm wide branched up to the 5^{th} order. It was the biggest studied colony, with a prominent bell-like holdfast 28 mm x 17 mm and the main stem being 8 x 6 mm in diameter near the base. Most of anterolateral pinnules of this specimen have up to six subpinnules arranged in subopposite pairs, the uppermost secondary pinnule when unpaired can be offset and almost perpendicular to the general plane of other secondaries. Skeletal spines of all pinnules were less compressed than in the holotype and do not exceed 0.2–0.22 mm in height (Fig. 4A–C). The paratype MNCN 2.04/2026 differs from the holotype in being a colony wider (31.5 cm) than high (26 cm), ramified in a single plane up to the 5th order, with a few small branches perpendicular to the main plane. First order branches reach up to 14.5 cm in length. Ramifications formed from the primary anterolateral pinnules (Fig. 2B) were observed. As occurs with the holotype, the main stem near holdfast is slightly compressed laterally (3.3 x 4.0 mm). There are 14–17 pinnules per 1 centimeter in four rows. Posterolateral pinnules reach up to 20 mm in length and 0.45 mm in basal diameter, while longest anterolateral primaries are 13 mm long and have a basal diameter of up to 0.44 mm. From 100 anterolateral pinnules examined in two third-order branches from the middle of the corallum, 3 % have two secondary pinnules, 29 % have three, 54 % have four, 13 % have five and 1 % has six. Spines agree with the holotype in shape, number of rows (3–5), size (up to 0.26 mm near the tip of primary pinnules), density (3–4 spines/mm on each alignment) and distance between spines of the same row (0.3–0.5 mm).

Additional material (Table 2). The sample at Concarneau Marine Station reference collection is a small dried colony 16.5 cm high and 18.5 cm wide branched in one plane to the second order and with very long basal secondary pinnules up to 15–18 mm on the anterolateral primary pinnules. MNHN-IK-2015-3171 (Grasshoff, 1982a, b) is a damaged colony without base branched to the third order without soft tissue and with broken posterolateral pinnules and anterolateral pinnules up to 10 mm. The specimen has more densely set primary pinnules with up to 17 pinnules in all rows per 1centimeter. Uppermost anterolateral secondary pinnule is often unpaired and perpendicular to the general plane. A juvenile colony from the Avilés Canyon (DR13-005-A0710) is only 11.5 cm in height, delicate, with a basal diameter of axis of 1.0 mm lacking side branches. Colony DR16-005-A0710 has several anterolateral pinnules with up to 6–7 subpinnules.

Comparisons. By the irregularly sparsely branching corallum, larger number of subpinnules per anterolateral pinnules (mostly 2–3 pairs vs 1–2) and form of spines the new species can be easily distinguished from *Trissopathes pseudotristicha* and *T. tetracrada* (see Table 1). *Trissopathes grasshoffi* sp. nov. is closely related to Indo-Pacific *T. tristicha*, but can be distinguished by the density of pinnules (12 pinnules in all rows per 1 centimeter in *T. tristicha* vs. 14–16 in new species) and also by the thicker posterolateral pinnules (0.35–0.4 vs. 0.2–0.3 mm) and anterolateral pinnules (0.35–0.45 vs. 0.25–0.26 mm) when comparing pinnules of the same length. The size and density, and number of rows of spines are similar in these two species, however, there is slight difference in form of spines (spines with visibly concave distal side in *T. tristicha* vs. with always practically straight distal side in the new species (Fig. 3A–C, 4A–C)).

Etymology. The species is named after Prof. Manfred Grasshoff (Senckenberg Museum), who reported the species for the first time as *Antipathes* spec. (Grasshoff 1982a, b) from the Bay of Biscay (MNHN-IK-2015-3171).

Distribution. The Bay of Biscay (Grasshoff 1982a, b, Altuna 2010, Van Den Beld *et al*. 2017, present publication), Galicia Bank (present publication), Porcupine Bank (present publication), Logachev Mounds (De Clippele *et al*. 2019) and the George Bligh Bank (Narayanaswamy *et al*. 2013), depths 280–1196 m.

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FIGURE CAPTIONS

FIGURE 1. *Trissopathes grasshoffi* sp. nov. Holotype MNHN-IK-2015-2212: A– general view of colony; B– close up; C– polyps at posterolateral pinnule; D– polyps at anterolateral pinnule, E– SEM of anterolateral pinnule. Scale bar: A– 5 cm, B– 1 cm, C-E– 2 mm.

FIGURE 2. *Trissopathes grasshoffi* sp. nov. Paratype MNCN 2.04/2026: A– fragment of a branch showing the typical arrangement of the four rows of pinnules; B– an anterolateral pinnule giving rise to a ramification from its distal end; C– close up of a branch showing the four rows of pinnules in front view; D-F– anterolateral pinnules with 3–5 subpinnules. DR13-005-A0710: G– anterolateral pinnule with 6 subpinnules. Scale bar: A, D-G: 2 mm; B, C: 4 mm.

FIGURE 3. *Trissopathes grasshoffi* sp. nov. SEM of skeletal spines Holotype MNHN-IK-2015-2212: A– posterolateral pinnule; B– anterolateral pinnule; C– anterolateral subpinnules. Scale bar: 0.5 mm.

FIGURE 4. *Trissopathes grasshoffi* sp. nov. SEM of skeletal spines Schizoparatype IORAS CNI00013. SEM of spines. A– posterolateral pinnule; B– anterolateral pinnule; C– anterolateral subpinnules. Scale bar: 0.6 mm.

TABLE 1. Comparison of known species of the genus *Trissopathes* (based on van Pesch 1914, Opresko 2003 and original observations).

	T. pseudotristicha Opresko, 2003	*T. tetracrada* Opresko, 2003	*T. tristicha* (van Pesch, 1914)	*T.grasshoffi* sp. nov.
Corallum	Planar	Bushy to planar with overlapping branches	Irregularly branched	Irregularly branched to planar
Branching order	>4	>7	2–3*	2–3, up to 5 in larger colonies
Anastomoses	Absent	Present	Absent	Absent
Primary pinnules density per 1 cm	12–14	Up to 14	12	14–16
Lateral/posterolateral pinnules	Inclined distally (50–70°) with inner angle 190–210°	Inclined distally (~60°) with inner angle 260–270°	Inclined distally (45–60°) with inner angle 180–200°	Inclined distally (45–60°) with inner angle 270–300°
Lateral/posterolateral pinnules length, mm	10–20 (up to 26)	10 (rarely up to 20), slightly longer than anterolateral	10–15	10–18 (up to 26)
Lateral/posterolateral pinnules basal diameter, mm	0.15	0.15–0.2	0.2–0.3	0.35–0.4
Lateral/posterolateral subpinnules	Present only at side branchlets forming from posterolateral pinnules	Present only at side branchlets forming from posterolateral pinnules	Usually absent	Present only at side branchlets forming from posterolateral pinnules
Anterior/anterolateral pinnules	In two distinct rows with inner angle ~ up to 20° or appeared to be in single row, perpendicular to the stem	In two distinct rows with inner angle ~ 50–60°, distal angle ~60°	Appeared to be in a single row, distal angle ~80°	In two distinct rows with inner angle ~ 20–30°, slightly inclined or almost perpendicular to the stem (distal angle 70–85°)
Anterior/anterolateral pinnules position	At the same level or just below corresponding posterolateral pinnule	At the same level or just above corresponding posterolateral pinnule	Just below corresponding posterolateral pinnule	At the same level or just below corresponding posterolateral pinnule
Anterior/anterolateral pinnules length, mm	5–10	~10, slightly shorter than anterior	Mostly 5–6, can be as long as posterolateral	6–10, rarely more

	T. pseudotristicha Opresko, 2003	*T. tetracrada* Opresko, 2003	*T. tristicha* (van Pesch, 1914)	*T.grasshoffi* sp. nov.
Anterior/anterolateral pinnules basal diameter, mm			0.25–0.26	0.35–0.45
Lateral/posterolateral subpinnules	Rarely present	Usually absent	Usually absent	Usually absent
Anterior/anterolateral subpinnules	Present at most anterolateral pinnules; slightly curved distally	Absent near the tips of branchlets, present at other parts of colony; almost straight	Present; slightly curved distally	Present; almost straight
Anterior/anterolateral subpinnules length, mm	5–15	5	Up 10 (basal) 5–7.5 (distal)	Up 15 (basal) 5–8 (distal)
Anterior/anterolateral subpinnules basal diameter, mm	0.15	0.1	0.18–0.20 (basal) 0.12 (distal)	0.25–0.28 (basal) 0.15 (distal)
Anterior/anterolateral subpinnules	In 1 subopposite pair; distal angle to anterolateral 60–70°	1–2 subpinnules: single at anterior side or in subopposite pair; distal angle to anterolateral 50-60°	In 2–3 subopposite pairs, upper secondaries shorter than basal; in one plane; distal angle to anterolateral 70–80° (basal), 50–60 (distal)**	In 1–3 subopposite pairs, uppermost subpinnule can be unpaired ; usually in one plane; distal angle to anterolateral subpinnules 85–80° (basal), 50–60°(distal) when unpaired the most distal pinnule can be perpendicular to the general plane of basal subpinnules
Anterior/anteriolateral tertiaries	Usually absent	Usually absent	Usually absent	Usually absent
Spines	Simple, smooth triangular to conical, equilateral on the lower (basal) parts of the pinnules, but becoming more distally inclined on the mid and upper sections; practically straight distal side	Simple, smooth, acute, often with concave distal side	Simple, smooth, conical to acicular, inclined distally, often with visibly concave distal side	Simple, smooth, inclined distally, practically straight distal side
Spines, mm	Up to 0.13 mm	0.08-0.10 mm tall	Up to 0.28 mm, polypar side taller	0.04–0.05 near the base of pinnules; up to 0.25 mm near the tips of primary and secondary pinnules
Spines rows	3–4	3–4	3–5	3–5
Spines, distance, mm	0.25 to about 0.4 mm; ~4 per 1 mm	0.2–0.6 mm; 3–4 per 1 mm	2–3 per 1 mm	0.3–0.8 mm; 2–4 per 1 mm
Polyps size, mm	2–3	2–3	2*(anterior subpinnule)	2–3.5
Polyps per 1 cm	3–4	3–4	NA	3–4

*holotype ZMA Coel 3005 is unbranched specimen 90 mm.

** additional material from Philippines (USNM 76953) have distal angle of basal subpinnules to anterolateral pinnule 85–80°and distal subpinnules 50-60° (Opresko 2003: Fig. 9c, d, 10e).

TABLE 2. *Trissopathes grasshoffi* n.sp., material studied. Type material in bold.

Collection, number	RV, survey, station	Locality	Latitude	Longitude	Depth (m)	Date	Material description
Holotype MNHN-IK-2015-2212 [shizoholotype IORAS CNI00014]	**RV *Pourquoi Pas?* BobEco ROV *Victor 6000* PL 469-47-7**	**Guilvinec Canyon (Bay of Biscay)**	**46°56.197'N**	**05° 21.252'W**	**928**	**18.09.2011**	**24 cm high and 18 cm wide on *L. pertusa***
Paratype MNHN-IK-2015-2214	**RV *Pourquoi Pas?* BobEco ROV *Victor 6000* PL 468-46-6**	**Croizic Canyon (Bay of Biscay)**	**46°22.864'N**	**04° 0.740'W**	**849**	**17.09.2011**	**18 cm high and 14 cm wide**
Paratype MNHN-IK-2015-2215	**RV *Pourquoi Pas?* BobEco ROV *Victor 6000* PL 469-47-7**	**Guilvinec Canyon (Bay of Biscay)**	**46°56.024'N**	**05°21.621'W**	**834**	**19.09.2011**	**22 cm high and 14 cm wide**
Paratype Ifremer Brest reference collection no number [schizopara~~holo~~types: NHMUK 2019. 29; IORAS CNI00013]	**RV *Polarstern* ARK-XIX-3a ROV *Victor 6000* PS64/293-1**	**Porcupine Bank**	**53°11.55' N**	**14° 47.13'W**	**760**	**14.06.2003**	**41 cm high and 22 cm wide on *L. pertusa***
Paratypes MNCN 2.04/2026	**RV *Cornide Saavedra* ECOMARG 2009 G05**	**Galicia Bank**	**42º28.398'N**	**11º28.47'W**	**859**	**23.07.2009**	**26 cm high and 31.5 cm wide on coral debris**
G05-001-BG0709	RV *Cornide Saavedra* ECOMARG 2009 G05	Galicia Bank	42º28.398'N	11º28.47'W	859	23.07.2009	30 cm high and 32 cm wide on *Madrepora oculata* L.
MNHN-IK-2015-3171	RV *La Perle* BIOGAS1 CM01	Bay of Biscay	01 47˚44'N	08˚51'W	1010	04.08.1972	Fragment 22 cm long
Ifremer Brest reference collection no number	RV *Pourquoi Pas?* BobEco ROV *Victor 6000* PL 468-46-6	Croizic Canyon (Bay of Biscay)	46°22.823'N	04°40.642'W	837	16.09.2011	Lower part of colony 18 cm long on *L. pertusa*

DR01-005-BG0810	RV *Thalassa* INDEMARES 2010 DR01	Galicia Bank	42º40.866'N	11º36.645'W	999	08.08.2010	2 small fragments
DR03-032-BG0810	RV *Thalassa* INDEMARES 2010 DR03	Galicia Bank	42º43.626'N	11º50.236'W	797	09.08.2010	1 fragment 11.8 cm long
DR06-002-BG0810	RV *Thalassa* INDEMARES 2010 DR06	Galicia Bank	42º39.779'N	01º56.963'W	920	11.08.2010	2 colonies (26 cm in height and 31.5 cm wide, no holdfast; 24.5 cm high and 18.5 cm wide); 2 small fragments; small epizoic Chirostylidae)
DR08-054-BG0810	RV *Thalassa* INDEMARES 2010 DR08	Galicia Bank	42º55.941'N	12º05.149'W	1196	13.08.2010	2 colonies (17.5 cm high and 11 cm wide on *M. oculata*; 35.5 cm high and 11 cm wide, no holdfast; epizoic Chirostylidae ?)
G05-007-BG0810	RV *Thalassa* INDEMARES 2010 G05	Galicia Bank	42º47.045'N	11º45.382'W	827	20.08.2010	2 colonies (18.5 cm high and 16.5 cm wide, no holdfast; 17 cm high and 16.5 cm wide, no holdfast; epizoic zoanthid)
G06-003-BG0811	RV *Thalassa* INDEMARES 2010 G06	Galicia Bank	42º49.126'N	11º46.592'W	903	04.08.2011	Broken colony (17.5 cm high and 13.5 cm wide, no holdfast)
DR04-028-A0410	RV *Thalassa* INDEMARES 2010 DR04	Avilés Canyon (Bay of Biscay)	43º55.948'N	05º45.727'W	700	26.04.2010	1 colony (20.5 cm high and 10 cm wide)
DR13-004-A0710	RV *Thalassa* INDEMARES 2010 DR13	Avilés Canyon (Bay of Biscay)	43º58.306'N	05º47.212'W	769	03.08.2010	1 colony (32.5 cm high and 12.5 cm wide, no holdfast)
DR13-005-A0710	RV *Thalassa* INDEMARES 2010 DR13	Avilés Canyon (Bay of Biscay)	43º58.306'N	05º47.212'W	769	03.08.2010	1 colony (11.5 cm high on a stone, not ramified)
DR16-005-A0710	RV *Thalassa* INDEMARES 2010 DR16	Avilés Canyon (Bay of Biscay)	44º01.509'N	05º42.898'W	928	05.08.2010	2 colonies (17 cm high and 9 cm wide and 21.7 cm high and 19 cm wide); 3 fragments; epizoic polychaetes

DR04-002-A0511	RV *Miguel Oliver* INDEMARES 2011 DR04	Avilés Canyon (Bay of Biscay)	43º59.584'N	05º43.915'W	593	04.05.2011	1 colony (34.5 cm high and 33 cm wide, no holdfast); 3 fragments; epizoic ophiuroidea
Concarneau Marine Station reference collection	RV *Eureka*	Bay of Biscay	48ºN	08º40'W	980	26.07.1992	16.5 cm high and 18.5 wide , holdfast lacking